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STUDIES IN THE DYNAMICS OF GENETICALLY VARIABLE POPULATIONS. II. GROWTH OF EXPERIMENTAL POPULATIONS OF *DROSOPHILA MELANOGASTER* EXPERIENCING INTENSE NATURAL SELECTION

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Although population biology originated from both population genetics and ecology, its genetical models usually neglect organismic ecology, while theoretical population dynamics largely ignores genetical variation. These two disciplines have been most successfully blended in the theory of "r and K selection" (MacArthur and Wilson, 1967; Pianka, 1970), for which the underlying genetics more recently has received theoretical investigation as "density-dependent natural selection" (Anderson, 1971; Anderson and King, 1970; Charlesworth, 1971; King and Anderson, 1971; Roughgarden, 1971; Charlesworth and Giesel, 1972b); and in the theory of "kin selection" (Hamilton, 1964; Wilson, 1975). Another, more restricted blend is "age-dependent selection" (Charlesworth, 1970, 1972; Charlesworth and Giesel, 1972a), which incorporates demographic theory into selection theory. Theoretical development of other areas remains spotty or of a largely superficial nature; that is, most theoretical population biology remains in the domain either of ecology or of population genetics.

There has been surprisingly little experimental investigation of these "hybrid" theories, though many observational data may be fit to them. Gadgil and Solbrig (1972) provided virtually the only experimental test of the theory of "r and K selection", and some of the few experimental investigations of "density dependent selection" (Birch, 1955; Bhalla and Sokal, 1964; Druger and Nickerson, 1972; Kojima and Huang, 1972; Lewontin, 1955; Lewontin and Matsuo, 1963; Moree and King, 1961; Sokal and Huber, 1963; Sokal and Karten, 1964; Sokal and Sullivan, 1963) yield ambiguous results (DeBenedictis, 1977). Elsewhere, the influence of population composition (DeBenedictis, 1978) and of variation in both population density and composition (DeBenedictis, 1977) on fitness and gene dynamics of flies in experimental populations of *Drosophila melanogaster* is described. This study reports the dual to these earlier findings: how population dynamics of these experimental populations were influenced by variation in their genetic composition.

Materials and Methods

Experimental populations of *Drosophila melanogaster* were synthesized from flies homozygous or heterozygous for fourth chromosomes marked by the recessive mutants in repulsion linkage: either by *sparkling-poliert* (hereafter *s*) or else by *cubitus-interruptus* and *shaven-naked* (hereafter *c;* for descriptions see Lindsey and Grell, 1968). These chromosomes exhibit the Mendelian genetics

of alleles of a single locus (Bundgaard and Christiansen, 1972; Prout, 1971a, b) for which homokaryotypes have a mutant phenotype and heterokaryotypes have a wild-type phenotype; Bundgaard and Christiansen (1972) detail ntness components for this system. Handling of cultures is described in DeBenedictis (1977, 1978). Briefly, flies were raised at 23°C with a 12-hr photoperiod on an agar-molasses-cornmeal medium in one-pint bottles. Contrived mixtures of virgin f_1 progeny from stock cultures became the parents of experimental cultures. After four days, parental flies were removed from experimental cultures and censused to sex and karyotype. Thereafter, the f_1 progeny of these parental flies were removed from cultures at four day sampling intervals until such time (20 days after initiation of cultures unless otherwise noted) that these progeny could have been contaminated by f_2 flies. The f_1 progeny were censused to sex and karyotype and then discarded. Discrete sampling times were adopted because they accord best with the genetical theory from which fitness was estimated and, except for constraints imposed by *Drosophila* biology, procedures for handling cultures were otherwise arbitrarily adopted.

Because selection was density-independent in this system (DeBenedictis, 1977), population density of adult flies was measured without regard to karyotype. Population growth was measured either as the total progeny obtained from all censuses of a culture, or as a finite population growth rate, λ. Although population age structure usually arises from successive births in a cohort of parents as those parents age, in the present study "age structure" arises because the offspring of a single age class of parents mature over several successive sample times. In either case, λ satisfies:

$$\lambda^{\beta+1} - \sum_{x=\alpha}^{\beta} \{B(t+x)/N(t)\}\,\lambda^{\beta-x} = 0$$

where α is the sample interval at which offspring first mature, β is the sample interval at which offspring last mature, $B(t+x)$ is the number of offspring obtained on the xth census after parents are removed from a culture, and $N(t)$ is the number of parents of those offspring. Total progeny and finite population growth rate were highly correlated; over 95% of the variation in $\ln(\lambda)$ could be attributed to variation in ln(total progeny/parent). The remaining variation reflects the spacing of "births" among the progeny obtained from a culture.

Wallace (1974) shows that *Drosophila* population dynamics exhibit "female dominance" (Keyfitz, 1969: chapter 13.2). Therefore, sex ratios (M/F) of progeny were also examined because the number of females in a cohort is a major determinant of that cohort's growth rate.

Five series of experimental cultures were set out from four sequential generations of stock cultures. Each experimental series had distinct goals, which are described below. In the following discussion "monomorphic" cultures produce only one karyotype of offspring, while "polymorphic" cultures yield all three karyotypes. Because population growth declined with increasing population density, null hypotheses generally were tested most effectively by analyses of covariance. Rejection level for null hypotheses was set at 0.05.

Results

Independence of the dynamics of successive generations

Experimental designs for this report assume that gene and population dynamics may be specified by measuring changes from a range of initial conditions over a single generation. Bundgaard and Christiansen (1972) and Prout (1971b) provide experimental verification that single generation adaptive value estimates predict gene dynamics of this and of similar genetic systems. Because mean size and, correlated therewith, fecundity of *Drosophila melanogaster* decreases with increasing crowding (Chiang and Hodson, 1950; Barker and Podger, 1970b), population growth potentially could be influenced by the crowding experienced by the previous generation even under otherwise uniform conditions (Shorrocks, 1970). To determine the importance of such effects, population dynamics in cultures descended from crowded or uncrowded stocks were compared. This series of cultures is hereafter called the *stocks experiment*. Stock cultures were initiated either with 25 or with 100 pairs of flies. From these stocks, cultures that would be monomorphic for *s/s*, *s/c*, *c/s*, and *c/c* karyotypes were established, in which parental density was varied from 25 to 100 pairs of flies. Although low productivity of crowded stocks precluded completion of a planned balanced experimental design, sufficient data were obtained to compare population dynamics of cultures descended from crowded *versus* uncrowded stocks by covariance analysis.

The number of surviving female parents was a better predictor of total progeny and of λ than were either total surviving parents or number of parents introduced to experimental cultures. Both total progeny and λ were exponential functions of the number of surviving female parents (Fig. 1). Neither measure, when adjusted for differences in the number of surviving female parents, was consistently influenced

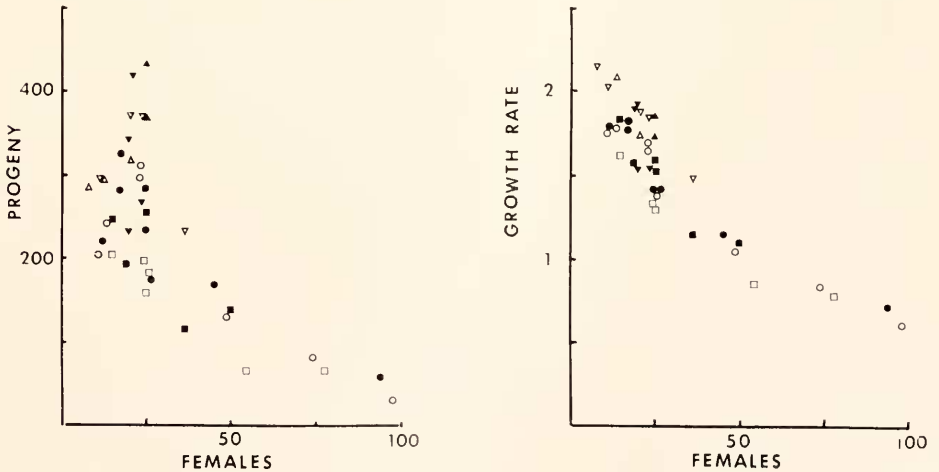

Figure 1. Total progeny (left) and finite population growth rate (right) as functions of female parental density, when parents derived from crowded (solid symbols) or from uncrowded (open symbols) stocks and cultures are monomorphic for: *s/s* (circles), *s/c* (triangles), *c/s* (inverted triangles), or *c/c* (squares).

TABLE I

Covariance analysis of the stocks experiment.

Source	Regression	
	Total Progeny	Finite growth rate
Uncrowded stocks	$P = 412 \exp(-0.0246N_t)$	$\lambda = 2.192 \exp(-0.0137N)$
Crowded stocks	$P = 386 \exp(-0.0195N_t)$	$\lambda = 2.188 \exp(-0.0132N)$
Common	$P = 399 \exp(-0.0235N_t)$	$\lambda = 2.194 \exp(-0.0135N)$
F, between slopes (d.f. = 1,35)	1.26	0.07
F, adjusted mean (d.f. = 1,36)	0.80	0.80

by the crowding experienced by stock cultures (Table I); *c/c* homokaryotypes from uncrowded stocks grew less rapidly than did other karyotypes from uncrowded stocks, while cultures begun with *c/c* females and *s/s* males from crowded stocks grew more rapidly than did the other karyotypes from crowded stocks.

The sex ratio of progeny averaged 1.07, a value not satistically different from 1, and was not influenced by the strain of fly tested, the crowding experienced by either stock cultures or by parental flies, nor did it vary consistently between censuses of progeny from a given experimental culture.

The absence of a demonstrable influence of the crowding experienced by stock cultures on population dynamics suggests that these dynamics are fundamentally Markovian in nature, and justifies use of single-generation parameter estimates to describe the dynamical behavior of this system.

Characteristics of karyotypes in isolation

Population growth parameters of the different karyotypes growing in isolation were measured in three different experiments, including the stocks experiment. A similar series of monomorphic cultures, set out from uncrowded stocks, was established to measure population dynamics of *s/s, s/c, c/s,* and *c/c* karyotypes over a broader range of initial population densities. In this series of cultures, hereafter called the *strains experiment,* parental flies were not recounted after being removed from cultures; insufficient virgin females were available to establish the full range of densities for cultures that produced heterokaryotypic offspring.

Heterokaryotypes are particularly difficult to characterize, because cultures do not remain monomorphic for a full generation. In the two experiments described above, the f_1 were either all homokaryotypes or else all heterokaryotypes, but parents of the latter were homokaryotypes (*s/s* × *c/c* or *c/c* × *s/s*). Properties of heterokaryotypic parents were measured in a small series of cultures initiated with *s/c* or *c/s* parents, set out from excess stocks of the density experiment (described below), and intended primarily to measure relative larval viability. These cultures, which constitute the *viability experiment,* were compared with cultures monomorphic for the two homokaryotypes that were established simultaneously.

Results of these three experiments were inconsistent, perhaps because different batches of medium and, sometimes, yeast were used. Population growth of all karyotypes in the viability experiment was much less vigorous than in the stocks or strains experiments. Numbers of progeny obtained from *D. melanogaster* cul-

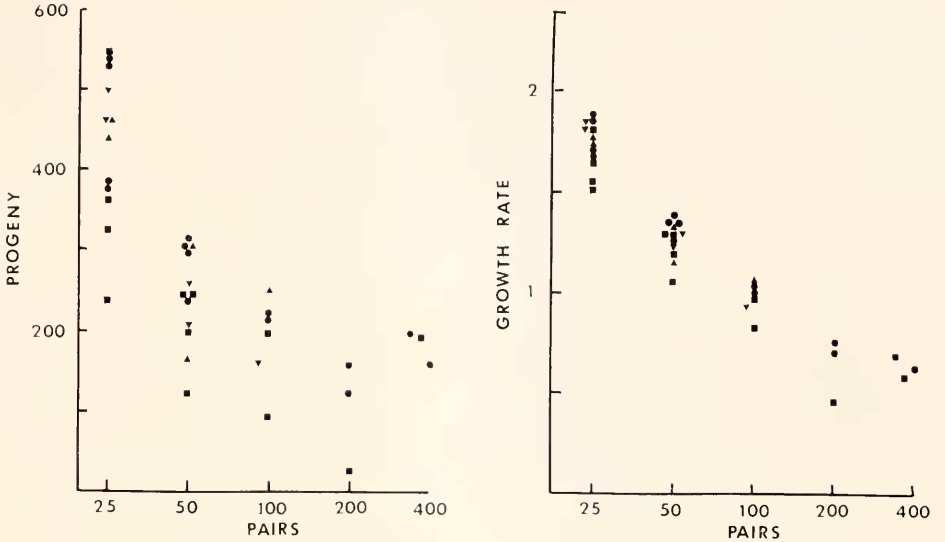

FIGURE 2. Total progeny (left) and finite population growth rate (right) as functions of the number of pairs of parental flies in the stocks experiment. Karyotypes indicated as in Figure 1.

tures commonly decline with crowding until some critical density is reached, after which increasing density may be accompanied by an increase in progeny number (Chiang and Hodson, 1950). The strains experiment spanned that critical density (Fig. 2), and regressions between progeny number or λ and log(parental density) were significantly curvilinear in this experiment only. However, even if higher density cultures in the strains experiment are ignored, its results remain distinct from the other two experiments.

In spite of these differences, two significant features were common to all experimental series. First, in each experiment, the regressions of initial density on total progeny or on λ for all karyotypes were parallel; only adjusted means (Table II) or, equivalently, carrying capacity differed. Writing these regressions as $y = a \exp\{\text{slope}\}$, the least squares estimates of the term, {slope}, common to all karyotypes are given in Table II. Secondly, within each experiment, the largest adjusted mean is statistically greater than the smallest adjusted mean; that is, some difference between the estimated carrying capacity of the several karyotypes was evident in every series. While more detailed examination of differences between adjusted means was impossible because of unequal sample sizes, no other differences were suggested in most instances (Table II). In general, *c/c* homokaryotypes tended to have the lowest carrying capacity, and heterokaryotypes are not markedly more successful than *s/s* homokaryotypes, as would be suggested by fitness differentials (DeBenedictis, 1977).

The sex ratio of progeny was not influenced by initial density of cultures but, in the stocks and in the strains experiments, it differed between strains. In the strains experiment, cultures producing *c/s* offspring only were slightly deficient in

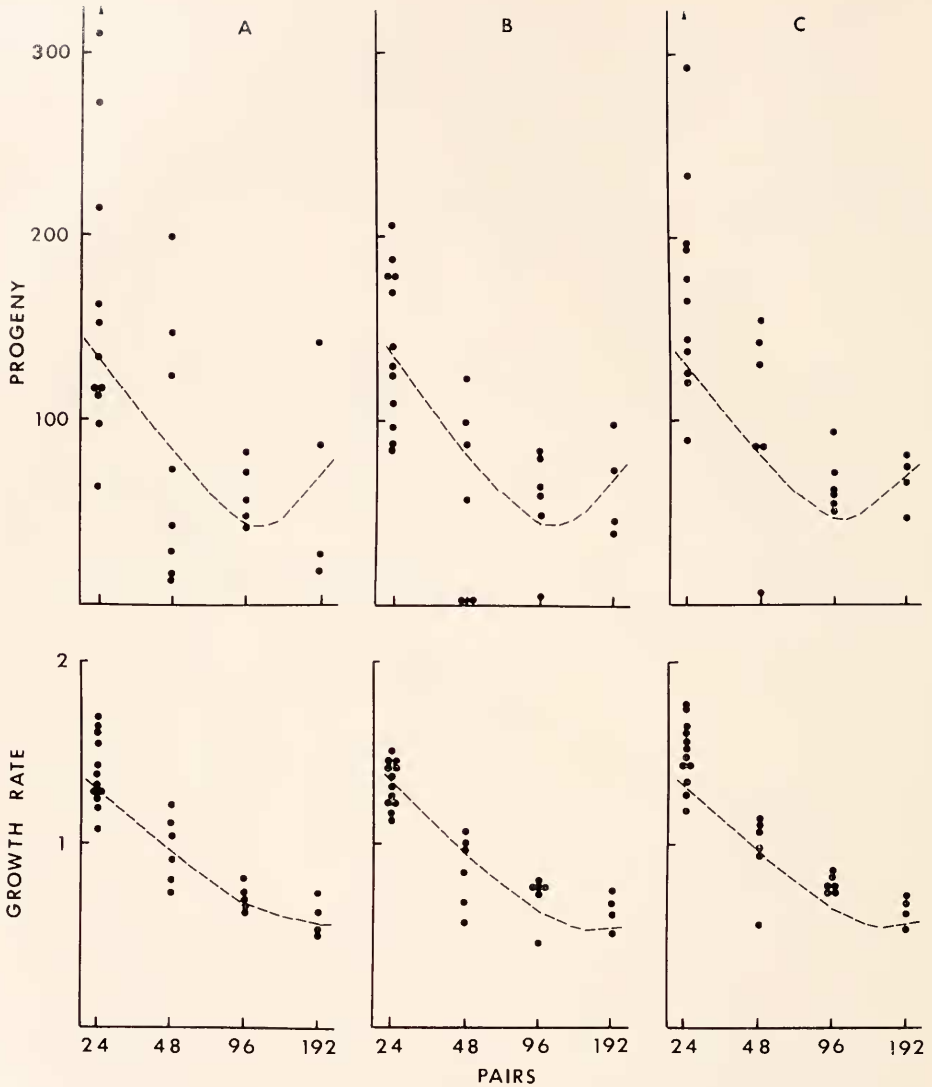

FIGURE 3. Total progeny (above) and finite population growth rate (below) as functions of the number of pairs of parental flies in the density experiment for three initial frequencies of *s* fourth chromosomes: A = 5/16, B = 8/16, C = 11/16. Dotted lines are the respective common (over initial fourth chromosome frequency) regressions for total progeny: $\ln(\text{progeny}+1) = 5.5050 - 0.0139N(t) + 0.000028N^2(t), (r^2 = 0.179)$ or for finite population growth rate: $\ln(\lambda) = 0.6168 - 0.0073N(t) + 0.000012N^2(t), \quad (r^2 = 0.788)$.

male progeny, while in the stocks experiment similar cultures produced a slight excess of male progeny. Ignoring these deviations, the sex ratio averaged 0.92 in the strains experiment, 1.07 in the stocks experiment, and 1.01 in the viability experiment; none of these values is statistically different from 1. Because estimates

TABLE II

Adjusted mean total progeny and finite population growth rate of karyotypes in monomorphic cultures.

Karyotypes	Experiment:		
	Strains	Stocks	Viability
	A. Total progeny		
s/s	291.4	197.9	129.6
c/c	191.1	157.9	108.7
s/c	267.4	271.8	—
c/s	252.5	258.2	—
Heterokaryotypic parents	—	—	77.9
{Slope}	$\{-0.008336N + 0.0000833N^2\}$	$\{-0.009806N\}$	$\{-0.002611N\}$
	B. Finite population growth rate		
s/s	1.2685	1.3455	.9881
c/c	1.1070	1.2564	1.0771
s/c	1.2174	1.4528	—
c/s	1 2244	1.4568	—
Heterokaryotypic parents	—	—	.8934
{Slope}	$\{-0.004638N + 0.00004098N^2\}$	$\{-0.005532N\}$	$\{-0.002930N\}$

N = number of parents introduced into cultures.

were variable and inconsistent between series, there is no compelling reason to assume the sex ratio of progeny of any of the genotypes is not 1 for purposes of population prediction.

The variation between experiments makes these results difficult to interpret (Cohen, 1976). The overall impression is that the karyotypes do not differ greatly from one another in the absence of interkaryotypic competition.

Population dynamics under selection

Dynamics of populations polymorphic for fourth chromosomes were measured in two experiments. The first of these, hereafter called the *composition experiment,* was intended primarily to measure the influence of population composition. Experimental design is detailed in DeBenedictis (1978). Briefly, seven mixtures of *s/s, s/c, c/s* and *c/c* karyotypes (Table III), each totaling 120 flies, were established. Cultures were censused as in the stocks experiment, except that censuses were continued through day 24 owing to the low productivity of cultures on the census taken on day 12. The seven experimental treatments were little altered by mortality of parental flies, and all converged toward a composition of about 60% *s* fourth chromosomes (DeBenedictis, 1978).

Most cultures in this series exhibited negative net population growth (Table III; Fig. 5). There were no detectable differences between treatments in the number of offspring obtained on any of the census dates, but there may be a difference

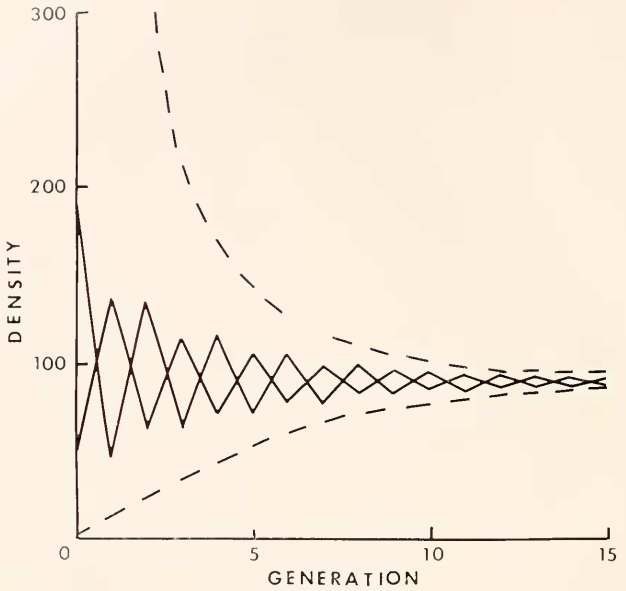

FIGURE 4. Representative discrete generation trajectories of populations obeying the rule: $N(t+1) = 245.9 \exp(-0.0139N(t) + 0.000028^2(t)) - 1$ (*cf.*, Fig. 3). Solid lines give trajectories for populations with $N(0) = 48$ or 192. Dotted lines indicate the regions within which all trajectories with $2 \leq N(0) \leq 548$ must lie.

in mean total progeny obtained/culture. No difference was detectable when ln(total progeny) were subject to analysis of variance, but the largest treatment mean was statistically greater than the three smallest treatment means (the latter means differ only from the largest) when (total progeny)$^{\frac{1}{2}}$ were subject to the same analysis; the log transformation produced somewhat more homoskedostic treatment variance. However, the largest mean finite rate of increase (Table III) was significantly different ($F_{6,52} = 2.39$, $P = 0.04$) from the smallest, and *vice versa*, although no other means were statistically distinct *a posteriori*. There was no obvious relationship between the composition of parental populations and any of these parameters.

TABLE III

Influence of population composition.

Parental population composition			Mean (± s.e.) progeny obtained on					Mean (± s.e.)
s/s	*s/c*	*c/c*	Day 12	Day 16	Day 20	Day 24	Total	
2	88	30	0.25 ± 0.15	10.8 ± 4.7	14.0 ± 4.5	20.9 ± 2.6	52.0 ± 7.0	0.8336 ± 0.0253
10	60	30	0.67 ± 0.35	11.9 ± 2.5	17.7 ± 2.5	23.0 ± 2.5	55.5 ± 6.3	0.8436 ± 0.0183
30	88	2	0.12 ± 0.12	14.4 ± 3.2	18.8 ± 3.4	23.5 ± 2.3	60.3 ± 5.3	0.8648 ± 0.0161
10	100	10	0.22 ± 0.14	10.2 ± 3.5	20.6 ± 2.9	26.9 ± 3.8	62.9 ± 7.2	0.8691 ± 0.0200
50	20	50	0.44 ± 0.32	16.0 ± 7.5	21.6 ± 2.3	27.6 ± 5.0	72.1 ± 2.9	0.8946 ± 0.0316
30	20	70	0.50 ± 0.25	17.3 ± 5.2	25.8 ± 2.2	24.0 ± 5.9	72.3 ± 10.5	0.8972 ± 0.0254
70	20	30	0.62 ± 0.35	27.3 ± 4.7	23.3 ± 3.8	34.2 ± 4.5	89.6 ± 6.4	0.9441 ± 0.0120

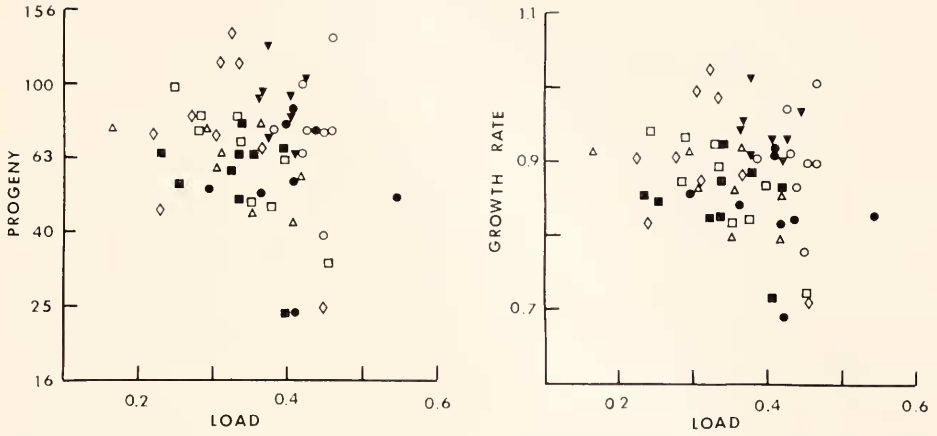

FIGURE 5. Total progeny (left) and finite population growth rate (right) versus theoretical genetic load for seven initial population compositions indicated as in Table III: open circles = 30/20/70; solid circles = 2/88/30; open squares = 10/100/10; solid squares = 30/60/30; open diamonds = 50/20/50; open triangles = 70/20/30; and solid triangles = 30/88/2. Loads differ between initial population compositions but are uncorrelated with total progeny or λ.

In the second experiment, hereafter called the *density experiment*, both population composition and density were varied. Experimental design and gene dynamics are described elsewhere (DeBenedictis, 1977). Briefly, experimental design was factorial, with three levels of the factor, population composition: 3/16, 8/16, and 11/16 frequency of *s* fourth chromosomes in parental flies; and with four levels of the factor, population density: 24, 48, 96 and 192 pairs of parental flies (Fig. 3). For genetical reasons (DeBenedictis, 1977) two series of cultures containing 24 pairs of parents were required; these were treated as separate levels of the factor density in analyses of variance. Each treatment at the highest density level had four replicates, while each treatment at the lower density levels had six replicates. Results from one anomalous culture were omitted.

Two-way analysis of variance of ln(total progeny + 1) and of ln(λ) revealed only initial population density to have detectably influenced their value (Fig. 3; Table IV). Crowded populations generally grew less rapidly than uncrowded

TABLE IV

Analyses of variance of the density experiment.

Source	d.f.	Mean square		
		Total progeny	Finite rate of increase	Sex ratio
Initial density	4	5.1160*	2.0399*	0.0448*
Initial composition	2	1.6837	0.0440	0.0087
Interaction	8	0.6401	0.0056	0.0034
Within treatment	68	0.6478	0.0218	0.0077

* Associated F-ratio has probability < 0.01 if treatment means are equal.

TABLE V

Analyses of covariance of the density experiment.

Adjusted mean	Initial frequency of sp^{spol} + + fourth chromosomes			Mean square		$F_{2,78}$
	0.3125	0.5000	0.6875	Between treatment	Within treatment	
Total progeny	99.65	67.40	106.88	0.3117	0.1245	2.543
Finite rate of increase	0.9933	0.9516	1.0296	0.0082	0.0043	1.923

populations but logarithmic regressions of initial density on total progeny and on λ were significantly curvilinear (Fig. 3), as in the strains experiment. Similar results apply to the number of progeny obtained on each census of these cultures. Covariance analysis supports these conclusions (Table V); no differences in adjusted means are detectable. Identity of these regressions implies that carrying capacity also was independent of population composition. Although only three levels of initial population composition were compared in this experiment, the range of compositions was nearly as great as in the composition experiment, and further, sample size for each composition was larger. The only reasonable conclusion from these results is that population composition has little influence on the population dynamics for this genetic system, even though these populations experienced intense natural selection.

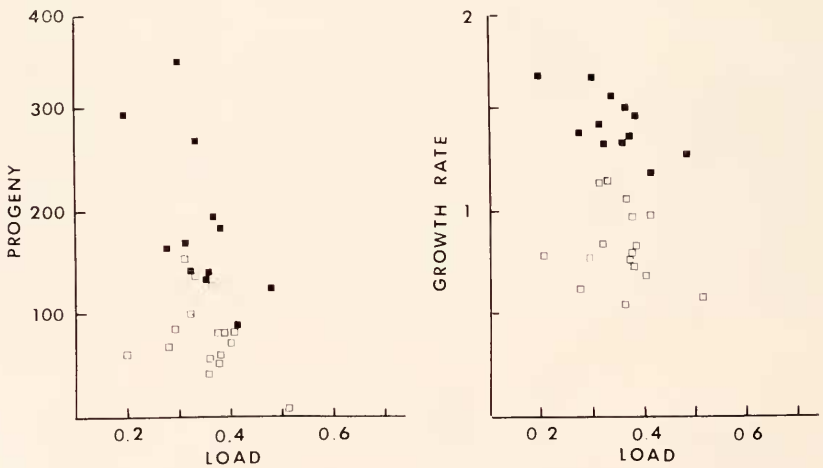

FIGURE 6. Total progeny (left) and finite population growth rate (right) *versus* theoretical genetic load in the density experiment for cultures initially with 11/16 *s* fourth chromosomes; solid squares are the lowest density level; open squares are the three higher density levels. If, as illustrated, the demographic variables are not adjusted to a common density, no relation exists; when adjusted to that expected from a common initial population density, a relation similar to that indicated by the solid squares exists. No correlation between load and demographic variables was evident in cultures that initially had 5/16 or 8/16 *s* fourth chromosomes in this experiment, even if demographic variables are adjusted for variation in initial population density.

The sex ratio was not influenced by initial population composition in the composition experiment ($F_{6,52} = 1.19$, $P = 0.33$), but its overall average of 1.21 was significantly > 1 ($t_{58} = 3.99$, $P < 0.001$). In the density experiment the sex ratio averaged 0.80, a value statistically < 1 ($t_{82} = -19.16$, $P < 0.001$), and was also influenced by initial population density (Table IV); sex ratios were highest but not distinguishable in cultures initiated with 24, 48 or 96 pairs of flies, but the sex ratio in cultures initiated with 192 pairs of flies was not distinguishable from that in cultures initiated with 48 pairs. Barker and Podger (1970a) also report skewed sex ratios, which were influenced by increasing population density, but their experimental design precludes more detailed comparison with the present results. Because sex ratios in these experiments deviated from unity in opposite directions, a constant sex ratio of 1 is assumed in the following discussion.

Discussion

Population dynamics in all experiments were most easily compared by adjusting mean parameter estimates to that corresponding to a constant initial density of 120 flies, the only density used in the composition experiment. This comparison revealed that population growth rates generally declined during the course of this study; they were lowest in the composition experiment. However, this difference cannot be attributed to the fact that in some experiments populations were monomorphic while in others they were polymorphic; population growth parameters in the density experiment (with polymorphic cultures) were indistinguishable from those in the viability experiment (with mostly monomorphic cultures). Barker and Podger (1972a, b) found that time influenced *Drosophila* population dynamics even within their experiments, and Wade (1977) provided data for a *Tribolium* system that exhibited a similar inexplicable decline.

Though variability of demographic parameters limits their utility in predicting growth, two features were consistent in all experiments. First, population growth declined with increasing population density. Secondly, because offspring percapita declined less rapidly than density increased, in very crowded cultures there was a slight increase in total offspring and in λ at the highest density levels, as in the strains (Fig. 2) and density experiments (Fig. 3). This second feature is also suggested in the other experiments where use of parabolic regression could not be statistically justified. Use of parabolic regressions for population prediction has two unrealistic features: they permit population growth when population density is 0 (or negative), and population size can expand indefinitely should it become sufficiently large. Fortunately, the empirical curves imply sufficiently strong population regulation that neither of these events can occur unless they are adopted as initial conditions. Further, it is likely that, were density increased beyond the levels tested in the present study, reproductive output would again decline with increasing crowding in this system.

Populations growing according to the empirical equations (Fig. 3) will approach a stable equilibrium density with oscillatory damping (May and Oster, 1976) whenever populations are initially small enough that "exponential" growth is not possible. If it were possible to reproduce consistently the environmental conditions under which these demographic parameters were measured, and if flies do not evolve

with respect to these conditions, discrete generation population growth may be predicted from the relations indicated in Figure 3; or from the equation: $\ln(\text{progeny} + 1) = 5.0725 - 0.0179N + 0.00003159N^2$ ($r^2 = 0.306$), which relates the number of offspring obtained between days 12 and 16 in the density experiment to parental density, N. This last equation represents discrete generation population dynamics better than does the equation for total progeny, since too few offspring matured before day 12 in high density cultures to permit use of the corresponding regression for population prediction. Depending on which equation is used, a population will converge, slowest for the above equation, to an equilibrium density of approximately 90 flies. Representative trajectories, and the limits within which all trajectories must lie provided $2 \leq N_o \leq 548$, are shown in Figure 4. These simulations ignore the great stochastic variation in reproduction output; Shorrocks (1970) ably discussed the influence of such variation.

Gene dynamics were utterly distinct. Adaptive values estimated from the composition experiment were consistent with those from the density experiment. Further, adaptive values proved quite sensitive to population composition but were uninfluenced by variation in population crowding (DeBenedictis, 1977, 1978). Simulation of gene dynamics predicted that genetic equilibrium effectively would be reached in a maximum of five generations over the range of population compositions tested in these experiments (DeBenedictis, 1977). These differences in response and in time scale indicate that gene and population dynamics were independent in this system, and are particularly interesting relative to genetic load theory (Crow, 1970; Crow and Kimura, 1970; Lewontin, 1974; Wallace, 1970).

Loads are usually measured by comparing inbred with randomly mated strains. The present study makes possible measurement of the effects of a "segregation" or

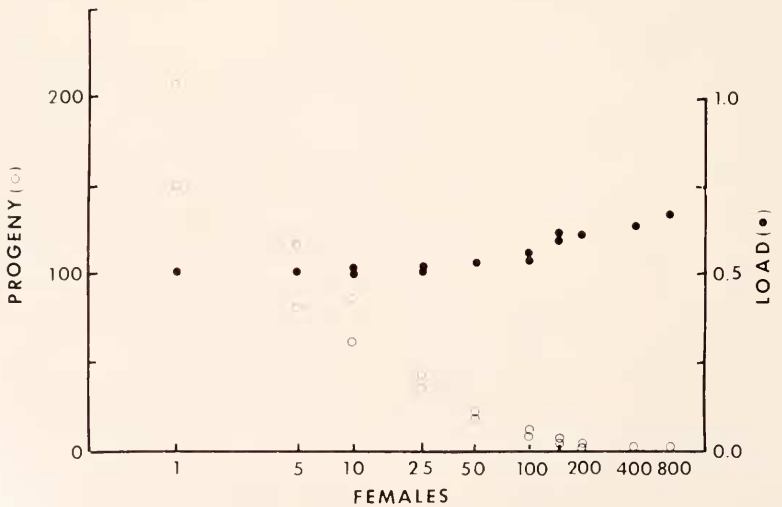

FIGURE 7. Mean total progeny/female parent (open circles) and mean segregational load (solid circles) as functions of initial female parental density for the *ebony* locus in *Drosophila melanogaster*. Values recalculated from Moree and King (1961: Table 3); dots indicating load for 1, 5, and 50 females represent two identical estimates.

"heterotic" (Wright, 1977) load for these *Drosophila* populations. The load, L = 1-w (Crow, 1970), was calculated from the adaptive values estimated in DeBenedictis (1977, 1978). The present report provides demographic characteristics for the same populations. If the load has an ecological impact, then total progeny and/or the finite growth rate should decline as the load increases. In the composition experiment loads calculated for the different initial population compositions (Fig. 5) were heterogeneous ($F_{6, 52} = 15.00$, $P < 0.001$). Within treatments the demographic parameters tended to decline as the calculated load increased, but only one correlation was statistically significant (Fig. 5); between treatments the demographic parameters tended to increase as the load increased, but the correlation was indistinguishable from 0. In the density experiment calculated loads were insensitive to initial population density ($F_{4, 68} = 1.35$) and there was no factor interaction ($F_{8, 68} = 2.05$); however, loads differed significantly between levels of initial population composition ($F_{2, 68} = 10.41$, $P < 0.01$). Expression of the load could be confounded by the dependence of population growth parameters upon population crowding (Fig. 6), unless these parameters are adjusted by covariance analysis to the values expected if all cultures had begun at a constant initial density. Such analysis revealed the expected relationship between load and dynamics only in cultures whose composition initially was 11/16 *s* fourth chromosomes (as in solid squares, Fig. 6); no correlation was evident between treatments. There has been no detectable influence of the "segregational load", other than changes in the genetic composition of these populations, even though the load may differ nearly two-fold between treatments.

While these results are anticipated by some theories, experimental substantiation is sparse because so few genetical studies have measured possible influences of crowding. Most of studies of density-dependent selection cited in the introduction to this report describe only larval viability. An investigation of the *ebony* locus of *Drosophila melanogaster* by Moree and King (1961) is the most nearly comparable study. Adaptive values, calculated as in DeBenedictis (1977, 1978), for their data were: $w_{+/+} = 0.92$; $w_{+/e} = 1$; and $w_{e/e}$ declined with population density. Because all parental flies in their study were heterozygotes, the load for these populations was $L = 0.73 - 0.25 w_{e/e}$ and increased with density. Population growth declined with increasing density, but because only one genetic composition was described, it is unclear to what extent this decline owed to ecological limits or to the increasing segregational load. If the load were the main determinant, then population growth, measured as mean progeny/parent, should decline in parallel with increases in selectional load. It did not (Fig. 7).

These examples could be criticized because they involve genes that disrupt the phenotype to an exceptional degree relative to most natural genetic variants, and because laboratory conditions shelter the organisms from natural environmental heterogeneity. Such criticism would be more important had a relationship between load and population dynamics consistently been evident, because the reduced effects of natural genetic variants and heterogeneity of natural environments may be invoked to explain how free-living populations tolerate their genetic loads. If one anticipates such mitigating effects, as most theory (*e.g.*, Levins, 1968) does, then the present experiments enhance the probability of observing any detrimental effects of a segregational load. If *D. melanogaster* can tolerate genes such as these under

"constant" laboratory conditions, then surely it can tolerate most natural genetic variants under natural conditions.

Genetic loads that accompany inbreeding depression often can be associated with fixation of genes whose deleterious effects are evident even in monomorphic cultures. The present study is quite different, because all three karyotypes involved theoretically can sustain vigorous monomorphic populations; indeed, the only difficulty is the biological impossibility of keeping heterokaryotype cultures monomorphic. Yet homokaryotypes are greatly disadvantaged in polymorphic cultures, and these *Drosophila* populations are responsive to population crowding. Why is there no load, and why are gene and population dynamics independent?

Frequency-dependent selection, although pertinent (DeBenedictis, 1977) and sometimes invoked to explain away loads, cannot be the explanation in this system. Not only was no load evident under nonequilibrium conditions, but a strong load is expected even under genetic equilibrium (DeBenedictis, 1977), as in several other genetic systems that exhibit frequency-dependent selection (DeBenedictis, 1978). Rather, the explanation seems to derive from the mechanism that produces frequency-dependent selection and from similar response of each karyotype to population crowding. Frequency-dependent selection appears to be generated almost entirely by female mating preferences: females reproduce essentially in proportion to their relative frequency and egg production is independent of the genotype of their mate, while the success of a male is strongly biased by its genotype (Bundgaard and Christiansen, 1972). Because biotic potential of the parents is not altered by this pattern of matings, differential mating success permits extensive genetic change without deleterious demographic consequences. Further, characterization of the karyotypes in isolation revealed that while their absolute (Darwinian) fitness declined with increasing crowding, the decline was parallel for all karyotypes. Therefore, their relative fitness, which determines the rate of genetic change, remained constant. Exactly the same behavior is evident in some other studies of "density-dependent selection" (notably Sokal and Huber, 1963; and Sokal and Karten, 1964), for which the published data also suggest no influence of crowding on the rate of gene change (DeBenedictis, 1977).

The theoretical explanation that seems to best apply to this system is "soft selection" (Wallace, 1968a, b, 1970, 1975). While these data appear to provide the clearest experimental validation of this concept, they must qualify Wallace's otherwise lucid expositions. The first point concerns the distinction between Darwinian fitness (mean offspring/parent) and relative fitness. Wallace correctly notes the ecological difference: Darwinian fitness of a population must equal or exceed one for a population to persist in time. However, his discussions do not sufficiently emphasize that it is the ratio of Darwinian (*i.e.*, relative) fitnesses that determines gene dynamics. Thus, given a set of relative fitness values, evolution occurs equally rapidly whether population size is expanding, declining, or constant. To that extent, the load is a mathematical artifact no matter how fitness is measured.

Wallace's emphasis on Darwinian fitness leads him (1975) to restrict "soft selection" to those cases in which selection is both frequency-dependent and density-dependent; and to restrict its opposite, "hard selection", to frequency- and density-independent selection. While the latter is necessarily true, "soft selection" should be more broadly applied to include all cases in which the only demographic responses

to natural selection are changes in the genetic composition of the population. This modified definition of soft selection with respect to frequency or density-dependent selection only blurs the distinction Wallace (1975) has made without challenging the essence of his discussion. By my criterion, the system described in this report is an example of frequency-dependent, density-independent selection which also exhibits "soft selection". Since it is conceivable that frequency-dependent, density-independent selection sometimes could influence the demography of populations, and since this is likely to be the case under density-dependent, frequency-independent selection, it will be necessary to examine a broader array of genetic systems to determine how widespread "soft selection" is.

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Summary

1. Growth of *Drosophila melanogaster* populations which were simultaneously subject to intense natural selection for marked fourth chromosomes was characterized in terms of number of progeny and a finite population growth rate.

2. There is no indication that the conditions experienced by past generations influenced the population growth potential of a cohort of adult flies; that is, population dynamics possess Markovian properties, justifying their characterization from observations of single-generation transitions.

3. The three karyotypes studied in this system exhibited parallel reductions in growth rates to increasing population density; they differed in "carrying capacity" or equilibrium density inconsistently and to a lesser degree than was suggested by adaptive values.

4. Experimental variation of the genetic composition of parental cohorts had almost no effect on population dynamics, but population growth rates declined markedly with increasing population density. Selection in this system has been found to be density-independent, but fitness of each genotype depends on population composition.

5. As a consequence of point 4, there is no discernable relationship between gene and population dynamics in this system. In particular, the theoretical "segregational load" and population growth rates were statistically uncorrelated.

6. This system is discussed in relation to the concept of soft selection. These data suggest that the definition of soft selection is less precisely related to the concepts of density-dependent and frequency-dependent selection than has been proposed.

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